Modelling short-term effects of sulphur dioxide.
2. Quantification of biochemical characteristics determining the effect of SO_2 on photosynthesis of leaves

M.J. KROPFF

Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, the Netherlands

Abstract

A summary version of a model for the SO_2 flux into leaves and effects of SO_2 on the rate of photosynthesis (Kropff, 1989) was used to analyse experimental data on the effects of SO_2 on the rate of photosynthesis with standard statistical techniques. Values for the two key parameters of the model, a sensitivity parameter relating intracellular S(IV) concentration (SO_2, bisulphite and sulphite) to photosynthetic reduction, and a time coefficient for S(IV) oxidation, were estimated from data on photosynthesis during fumigation and subsequent recovery period, by combined non-linear regression of both equations.

The pattern of rapid photosynthetic reduction by SO_2 and rapid recovery following fumigation was accurately described with the model for several data sets. Parameter estimates agree very well with experimentally determined values. It is concluded that differences in photosynthetic sensitivity of plants are mainly due to differences in the time coefficient for sulphite oxidation. Variation in leaf thickness may also have contributed to the differences in sensitivity. This approach can be used to parameterize the model for short-term effects of SO_2 on leaf photosynthesis for specific species and environmental conditions from easily obtained data.

Additional keywords: stomatal behaviour, simulation model, sulphur metabolism, pollution.

Introduction

A model was presented earlier, simulating SO_2 flux from the atmosphere into leaves and the effects of toxic SO_2 metabolites on the rate of photosynthesis and on stomatal resistance (Kropff, 1989). The model contains two key parameters, a sensitivity parameter relating photosynthetic reduction to intracellular S(IV)* concentration, and a time coefficient for S(IV) oxidation determining the rate of S(IV) removal to the less toxic sulphate. The sensitivity parameter was derived from experimental data on photosynthetic reduction in relation to the intracellular S(IV) concentration from Sakaki and Kondo (1985) who used isolated protoplasts and chloroplasts of *Vicia faba* L., and Alscher et al. (1987) who studied the effects of SO_2 exposure on two cultivars of *Pisum sativum* L. Other data sets on both effects on photosynthesis and S(IV) concentrations were not available

---

* S(IV) = $[SO_2]_{aq}$ + $[HSO_3^-]$ + $[SO_3^{2-}]$

in literature. Surprisingly, the same relationship between reduction in the rate of photosynthesis and internal sulphite concentration was observed for both data sets (Kropff, 1989). Especially the results of Alscher et al. (1987) suggest that differences in sensitivity for SO_2 between plants is not based on differences in the sensitivity of photosynthesis to internal S(IV). Instead, they suggest that these differences are primarily based on the capacity of leaves to remove the toxic S(IV) by oxidation, or on differences in leaf thickness, since it determines the internal concentration at a given SO_2 flux density. The time coefficient for S(IV) oxidation varies strongly between species and cultivars (Miller and Xerikos, 1979; Alscher et al., 1987). Rothermel and Alscher (1985) observed that the rate of S(IV) oxidation strongly depended on the light intensity, indicating that environmental conditions may influence the rate of S(IV) oxidation.

Quantification of the relationship of biochemical parameters to environmental factors is essential for the prediction of SO_2 uptake by leaf canopies and effects on canopy photosynthesis, using crop growth models extended with submodels for the effects of SO_2. Such combination models may help to elucidate and predict the effects of SO_2 on crops and vegetation over an entire growing period.

For experimental determination of S(IV) in plants during the exposure of leaves to realistic SO_2 concentrations ($< 200 \mu g \ SO_2 \ m^{-3}$), biochemical methods are needed to detect very low S(IV) concentrations in leaf tissue [< 0.05 mmol S(IV) l^{-1}] (Kropff, 1989; Huber et al., 1987). However, the detection limit is about 0.04 mmol S(IV) l^{-1} (Huber et al., 1987) and experimental determination in leaf tissue is extremely difficult because S(IV) quickly oxidizes to sulphate.

In order to gain more insight in the quantitative values of these two parameters, the model presented in a preceding paper (Kropff, 1989) was fitted to experimental data on the short-term effects of SO_2 on photosynthesis of various species.

Materials and methods

Theory

Determining biochemical characteristics from the time course of the rate of photosynthesis during exposure of a leaf to SO_2 and subsequent recovery. The SO_2 flux into the leaf, the sulphur balance in the leaf and the effects of toxic SO_2 metabolites on photosynthesis in their simplest form can be described by four equations. A detailed description of the backgrounds is given by Kropff (1989). The sum of resistances to CO_2 (consisting of the stomatal and boundary layer resistance r in s m^{-1}) can be derived from the rate of photosynthesis (P, g CO_2 m^{-2} s^{-1}) and the difference between ambient and internal CO_2 concentrations ($C_a - C_i$, g CO_2 m^{-3}), which tends to be constant at a given CO_2 concentration, even during SO_2 exposure (Kropff, 1987):

$$r = \frac{C_a - C_i}{P} \qquad (1)$$

The SO_2 flux into the leaf (F, mmol SO_2 m^{-2} s^{-1}) can be calculated from the ambient SO_2 concentration (mmol SO_2 m^{-3}) and the leaf resistance for SO_2 (ca. 1.2 r for CO_2), assuming the internal SO_2 concentration to be 0 (Black and Unsworth, 1979; Carlson, 1983; Kropff, 1989):

$$F = \frac{S_a}{1.2\,r} \tag{2}$$

The change in the internal S(IV) (mmol S(IV) l^{-1}) depends on the SO_2 flux into the leaf and rate of S(IV) removal by oxidation of S(IV) to the less toxic sulphate:

$$\frac{dS(IV)}{dt} = \frac{F}{d} - \frac{S(IV)}{\tau_2} \tag{3}$$

where τ_2 is the time coefficient (s) for S(IV) oxidation (first order reaction) and d is the leaf thickness (mm). The effects of internal S(IV) on the rate of photosynthesis can be described with a linear relation of S(IV) concentrations up to 0.8 mmol S(IV) l^{-1} (Kropff, 1989), or reduction in the rate of photosynthesis of less than 60% (Kropff, 1989):

$$P = P_0\,(1 - kS(IV)) \tag{4}$$

P_0 denotes the rate of photosynthesis before fumigation, P the actual rate of photosynthesis and the parameter k expresses the sensitivity of the rate of photosynthesis of the S(IV) concentration in [mmol S(IV) l^{-1}] $^{-1}$ or in [mmol S(IV) m^{-2}] $^{-1}$, when leaf thickness is not known.

Combining these four equations gives an expression for the first derivative of the S(IV) concentration with respect to time:

$$\frac{dS(IV)}{dt} = \frac{S_a P_0}{1.2\,(C_a - C_i)\,d} - \left[\left(\frac{S_a P_0 k}{1.2\,(C_a - C_i)\,d} + \frac{1}{\tau_2}\right)S(IV)\right] \quad ; \quad t < t_e \tag{5}$$

where t_e is the moment at which fumigation is stopped. This equation can be abbreviated by introducing another time coefficient (τ_1, s):

$$\tau_1 = \frac{1.2\,(C_a - C_i)\,d}{S_a P_0 k} \tag{6}$$

Eqn 5 then becomes:

$$\frac{dS(IV)}{dt} = \frac{1}{\tau_1 k} - \left(\frac{1}{\tau_1} + \frac{1}{\tau_2}\right)S(IV) \quad ; \quad t < t_e \tag{7}$$

Eqn 7 can be analytically solved (with an initial S(IV) concentration of 0) giving an expression for the time course of S(IV) during exposure of the leaf to SO_2:

$$S(IV) = \frac{\frac{1}{\tau_1 k}}{\frac{1}{\tau_1} + \frac{1}{\tau_2}}\,[\,1 - e^{-t\left(\frac{1}{\tau_1} + \frac{1}{\tau_2}\right)}\,] \quad ; \quad t < t_e \tag{8}$$

in which t is the time after the start of fumigation. In combination with Eqn 4 this gives an expression for the relative rate of photosynthesis (P/P_0, P_0 denotes the rate of photosynthesis before fumigation, P is the actual rate of photosynthesis in time after the start of fumigation:

$$\frac{P}{P_0} = \frac{T_1}{T_1 + T_2} + \frac{T_2}{T_1 + T_2} e^{-t\left(\frac{T_1 + T_2}{T_1 T_2}\right)} \quad ; \quad t < t_e \quad (9)$$

When SO_2 exposure is terminated, another relationship for the rate of photosynthesis has to be used. Eqn 5 is much simpler in clean air since the ambient SO_2 concentration is 0:

$$\frac{dS(IV)}{dt} = \frac{S(IV)}{T_2} \quad ; \quad t > t_e \quad (10)$$

An expression for the S(IV) concentration can be derived from analytical solution of Eqn 10:

$$S(IV) = S(IV)_{t_e} e^{-\left(\frac{t - t_e}{T_2}\right)} \quad ; \quad t > t_e \quad (11)$$

where t_e is the moment at which fumigation is stopped. Combination of Eqn 11 with Eqn 4 gives an expression for the relative rate of photosynthesis during the recovery period:

$$\frac{P}{P_0} = 1 - \left[1 - \left(\frac{P}{P_0}\right)_{t_e} \right] e^{-\left(\frac{t - t_e}{T_2}\right)} \quad ; \quad t > t_e \quad (12a)$$

where t is the time since the onset of the exposure and $(P/P_0)_{t_e}$ is the relative photosynthesis at the end of the exposure period. $(P/P_0)_{t_e}$ can be found from Eqn 9, which results in:

$$\frac{P}{P_0} = 1 - \left[1 - \frac{T_1}{T_1 - T_2} - \frac{T_2}{T_1 + T_2} e^{-t_e\left(\frac{T_1 + T_2}{T_1 T_2}\right)} \right] e^{-\left(\frac{t - t_e}{T_2}\right)} \quad ; \quad t > t_e \quad (12b)$$

Using a non-linear regression procedure ('OPTIMIZE' in GENSTAT IV, Alvey et al., 1982), the two equations (Eqns 9 and 12b) can simultaneously be fitted to experimental data in which gas exchange is measured during a fumigation period and a subsequent recovery period. This procedure gives estimated values for T_1 and T_2. From the estimated value of T_1 the value of the sensitivity parameter k can be calculated with Eqn 6, when P_0, S_a, C_a and C_i are known [k in (mmol S(IV) m^{-2} leaf)$^{-1}$ or in (mmol S(IV) l^{-1})$^{-1}$, when the leaf thickness is known].

When stomata do not respond to a reduced photosynthesis (e.g. Alscher et al., 1987), a different set of equations has to be used (see Appendix).

Relating biochemical parameters and the relationship between the rate of photosynthesis and SO₂ uptake in equilibrium situations. The presented set of equations and parameters can be easily related to direct measurements of SO_2 uptake rate and relative photosynthesis in equilibrium situations. The two important parameters τ_2 and k [(mmol S(IV) m^{-2})$^{-1}$] can be included in one expression by combining Eqn 3 (in which the change in S(IV) concentration is set to 0, since the S(IV) concentration is stable) with Eqn 4 which relates SO_2 uptake rate and the effect on relative photosynthesis:

$$\frac{P}{P_0} = 1 - k\tau_2 F \qquad (13)$$

where F is the rate of SO_2 uptake in mmol SO_2 m^{-2} s^{-1}. Kropff (1987) showed that the relationship between SO_2 uptake and reduction of photosynthesis in equilibrium at light saturation of *Vicia faba* leaves can be described by:

$$\frac{P}{P_0} = 1 - qF \qquad (14)$$

where q is the slope and equals $k \tau_2$, when k is expressed in (mmol S(IV) m^{-2})$^{-1}$.

Experimental data

Several experimental data sets on relative photosynthesis during a short fumigation period and subsequent recovery, were used to analyse model behaviour and to quantify biochemical characteristics. Bennet and Hill (1973) measured the effect of SO_2 on photosynthesis of 4-8 week old barley plants (*Hordeum vulgare* L., cv. Trebi). The effect of 675 and 1080 µg SO_2 m^{-3} was measured for two hours after the start of fumigation and a recovery period of two hours. Sij and Swanson (1974) analysed the effects of much higher SO_2 concentrations (2700-13 500 µg SO_2 m^{-3}) on bean leaves (*Phaseolus vulgaris* L.) for a one-hour fumigation period and a subsequent recovery period of two hours. A very extensive data set on photosynthesis of several plant species (*Vicia faba* L., cv. Three fold white and cv. Blaze; *Lolium perenne* L., cv. S23; *Hordeum vulgare* L., cv. Sonja; *Triticum aestivum* L., cv. Virtue and *Brassica napus* L., cv. Rafal.), influenced by a large range of SO_2 concentrations (270, 540, 810, 1080 and 1350 µg SO_2 m^{-3} respectively) was published by Darrall (1986). The first three species were grown in the glasshouse and the second group was grown outdoors. The plants grown outdoors were much less sensitive to SO_2 than plants grown in the greenhouse. Finally, a data set on leaves of *Vicia faba* L. cv. Minica exposed to 810 and 1600 µg SO_2 m^{-3} was used (Kropff and Smeets, unpublished) for methods see Kropff (1987). Absolute rates of photosynthesis before the start of fumigation (P_0) and internal CO_2 concentrations needed to calculate the sensitivity parameter k, were estimated when they were not reported.

Results and discussion

Determining biochemical characteristics from the time course of the rate of photosynthesis during exposure of a leaf to SO_2 and subsequent recovery. The combination

218

of Eqns 9 and 12b was fitted to experimental data on photosynthesis during fumigation and recovery to estimate values for the parameters τ_1 and τ_2 can also be estimated from the rate of photosynthesis during fumigation only. However, when both the fumigation and recovery period are used, more information on model behaviour in relation to the real system is obtained and the interdependence of the estimated parameter values is reduced.

The results of fitting the model to the experimental data from Darrall (1986), Bennet and Hill (1973), Sij and Swanson (1974) and the data set with broad bean are presented in Fig. 1. The pattern of a rapid reduction after the start of the exposure and the fast recovery after the fumigation period was described very satisfactorily by the model for all data sets. Both the time course of the rate of photosynthesis during and after exposure were accurately described by the model with one set of parameters. This indicates that short-term effects can be well described on the basis of the proposed mechanism. Unreliable estimates of the parameters were determined when reductions in the rate of photosynthesis were very low ($< 5\%$). Relative photosynthesis during the recovery period was not described correctly at very high SO_2 concentrations only, indicating that mechanisms other than a reversible inhibition of photosynthesis by S(IV) played an important role as well (*Vicia faba* L. cv. Blaze at 1350 μg SO_2 m^{-3} and *Phaseolus vulgaris* at 13 500 μg SO_2 m^{-3}).

The estimated parameter values are given in Table 1. Since leaf thickness is unknown for the experimental data used here, k expresses the relative reduction of photosynthesis per unit of S(IV) per unit leaf area, instead of per unit leaf volume. The values for k, are in the same range as the 0.832 (mmol S(IV) l^{-1})$^{-1}$ (Kropff, 1989), determined from the measurement of Alscher et al. (1987) and Sakaki and Kondo (1985). When leaf thickness equals 0.5 mm, k is 1.664 (mmol S(IV) m^{-2})$^{-1}$ and at 0.2 mm, k equals 4.16 (mmol S(IV) m^{-2})$^{-1}$. This indicates that differences in the determined values of k may possibly be explained on the basis of differences in leaf thickness, i.e. the *Hordeum* plants of Darrall (1986) were grown outside, whereas the other species were grown indoors, where plants normally have thinner leaves.

Large differences were observed in the time coefficient for S(IV) oxidation, which confirms the results of Alscher et al. (1987) that the rate of sulphite oxidation determines the sensitivity of species. The differences in sensitivity between *Hordeum vulgare* and the other species examined by Darrall (1986) seems to be caused by large differences in the rate of S(IV) oxidation in combination with differences in leaf thickness.

This illustrates the necessity of working in well defined conditions, since both oxidation potentials of leaves and leaf thickness are determined by growth conditions. These data indicate that field-grown plants are less sensitive to air pollutants than plants grown in the greenhouse or phytotron. The time coefficient for S(IV) oxidation in some plant species (*Vicia faba* cv. Blaze, *Lolium perenne* and *Phaseolus vulgaris*) increases with increasing SO_2 concentration, indicating an additional (irreversible) effect. The sensitivity of plants clearly increases with increasing time coefficient for S(IV) oxidation (Table 1; Fig. 1).

The estimation of the parameters from literature data is inaccurate, because only means are reported in literature, without stanard errors, and the data necessary to calculate k (see Eqn 6) are rarely reported accurately. The best procedure for estimation of the parameters will be the determination of the parameters for data on individual plants, which allows the estimation of the variation in k and τ_2 in plants from

Relative photosynthesis (%)

Time (minutes)
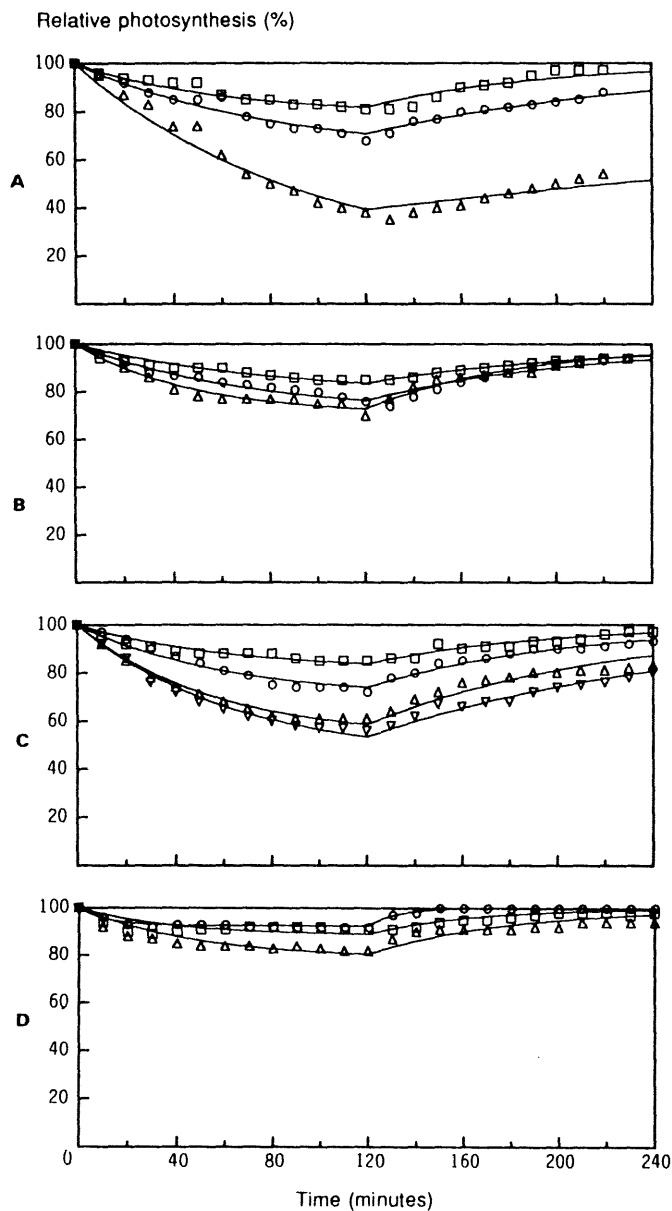
replicates. This procedure will be followed in a next paper, which deals with the effect of temperature and humidity on photosynthetic depression during SO_2 exposure.

Relating biochemical parameters and the relationship between the rate of photosynthesis and SO_2 uptake in equilibrium situations. The parameter values derived for broad bean (Table 1) were related to direct measurements of the SO_2 uptake rate and the rate of photosynthesis with Eqns 13 and 14. The parameter values derived from

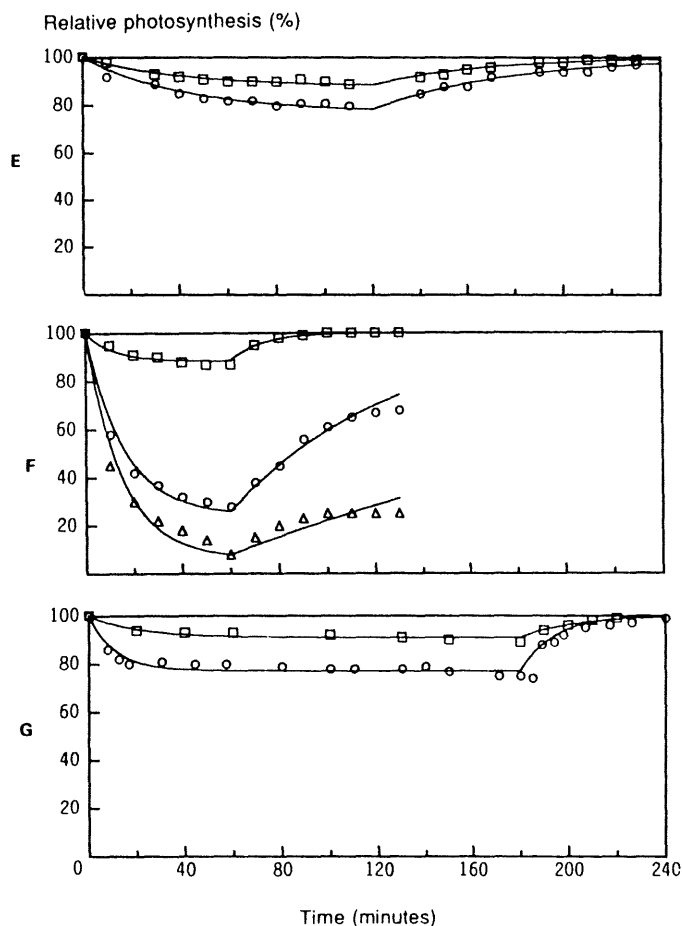Relative photosynthesis (%)

Time (minutes)

Fig. 1. Observed relative photosynthesis of single leaves during fumigation (2-3 h) and a subsequent recovery period (markers), and fitted relations with the model (lines). Parameter values are listed in Table 1. Data from Darrall, 1986:

a) *Vicia faba* cv. Blaze (□ 810 μg SO_2 m^{-3}; ○ 1080 μg SO_2 m^{-3}; △ 1350 μg SO_2 m^{-3});

b) *Vicia faba* cv. Three fold white (□ 810 μg SO_2 m^{-3}; ○ 1080 μg SO_2 m^{-3}; △ 1350 μg SO_2 m^{-3});

c) *Lolium perenne* cv. S23 (□ 540 μg SO_2 m^{-3}; ○ 810 μg SO_2 m^{-3}; △ 1080 μg SO_2 m^{-3}; ▽ 1350 μg SO_2 m^{-3});

d) *Hordeum vulgare* cv. Sonja (□ 810 μg SO_2 m^{-3}; ○ 1080 μg SO_2 m^{-3}; △ 1350 μg SO_2 m^{-3}). Data from Bennet and Hill, 1973;

e) *Hordeum vulgare* cv. Trebi (□ 675 μg SO_2 m^{-3}; ○ 1080 μg SO_2 m^{-3}). Data from Sij and Swanson, 1974;

f) *Phaseolus vulgaris* (□ 2700 μg SO_2 m^{-3}; ○ 8700 μg SO_2 m^{-3}; △ 13500 μg SO_2 m^{-3} and

g) *Vicia faba* cv. Minica, unpublished (□ 810 μg SO_2 m^{-3}; ○ 1600 μg SO_2 m^{-3}).

Table 1. Estimated values for τ_1 and τ_2 (minutes) with standard error and k, calculated from τ_1 (mmol S(IV) m^{-2})$^{-1}$. SO$_2$ concentration in μg SO$_2$ m^{-3}.

	SO$_2$ (μg m^{-3})	τ_1 (minutes)	SE	τ_2 (minutes)	SE	k (mmol S(IV) m^{-2})$^{-1}$
Vicia faba (cv. Blaze)	810	277.2	20.3	72.7	6.5	2.1
(Darrall, 1986)	1080	213.0	9.1	128.2	8.6	1.9
	1350	110.4	5.1	533.9	98.5	3.3
Vicia faba (cv. Three fold	810	367.7	18.5	96.5	6.7	1.1
white) (Darrall, 1986)	1080	237.3	11.8	93.1	6.0	1.4
	1350	159.1	6.9	66.5	3.3	1.7
Lolium perenne (Darrall,	540	320.9	19.5	74.9	5.6	2.1
1986)	810	196.4	7.9	84.4	4.2	2.3
	1080	117.1	4.8	101.9	5.1	2.9
	1350	114.0	3.2	135.5	5.1	2.3
Hordeum vulgare (1)	810	335.1	60.2	43.1	8.8	1.2
(Darrall, 1986)	1080	150.9	10.5	12.7	0.9	2.2
	1350	224.3	23.9	59.5	7.4	1.2
Hordeum vulgare (2)	675	339.6	16.2	46.0	2.5	2.1
(Bennet and Hill, 1973)	1080	188.3	8.6	56.1	2.9	2.3
Phaseolus vulgaris	2700	99.1	11.4	13.3	1.6	1.7
(Sij and Swanson, 1974)	8100	20.7	1.2	66.1	3.4	2.7
	13500	15.9	1.32	238.2	26.8	2.1
Vicia faba (cv. Minica)	810	231.7	24.1	23.1	2.3	2.2
	1600	48.7	5.7	14.4	1.7	2.9

data on the rate of leaf photosynthesis during SO$_2$ exposure (Kropff, 1989) are in close agreement with the observed relationship between the rate of photosynthesis and SO$_2$ uptake rate after two hours of exposure. The value for q was estimated to be 0.05 (μg SO$_2$ m^{-2} s^{-1})$^{-1}$ for this series of measurements. The values for τ_2 and k are given in Table 1 (τ_2 = 1380 seconds and k = 2.25 (mmol S(IV) m^{-2})$^{-1}$), resulting in ($k\,\tau_2$ =) 3105 (mmol SO$_2$ m^{-2} s^{-1})$^{-1}$ or 0.048 (μg SO$_2$ m^{-2} s^{-1})$^{-1}$. Leaf thickness was 0.4 mm for the plants used. The k value calculated from Table 1 (2.25 × 0.4 = 0.915 (mmol S(IV) l^{-1})$^{-1}$ is in agreement with k estimated from data of Alscher et al. (1987) and Sakaki and Kondo (1985) (Kropff, 1989).

Acknowledgements

222

Appendix

A model for the effects of SO_2 on photosynthesis when stomata do not respond to a reduced photosynthesis

When photosynthesis is depressed, but stomatal resistance remains unchanged during SO_2 exposure (Alscher et al., 1987), Eqns 9 and 12b cannot be used to analyse experimental data, because stomatal closure is assumed in this set of equations.

The main difference in the basic set of Eqns 1-4 is the substitution of P by P_0 in Eqn 1. Following the same procedure as described in the text, Eqn 9 then becomes:

$$\frac{P}{P_0} = 1 - \frac{T_2}{T_1}\left(1 - e^{\frac{-t}{T_1}}\right) \qquad ; \qquad t < t_e \qquad (15)$$

Eqn 12a remains unchanged. For Eqn 12b the following expression can be derived by combination of Eqns 12a and 15:

$$\frac{P}{P_0} = 1 - \left[\frac{T_2}{T_1}\left(1 - e^{\frac{-t_e}{T_1}}\right)\right] e^{-\left(\frac{t - t_e}{T_1}\right)} \qquad ; \qquad t > t_e \qquad (16)$$

Calculation of k can be performed with Eqn 6.

Samenvatting

Simulatie van de korte termijn effecten van zwaveldioxide. 2. Kwantificeren van biochemische karakteristieken die het effect van SO_2 op de fotosynthese bepalen

Een model voor de flux van SO_2 in het blad, het metabolisme van SO_2 in het blad en de effecten van SO_2-metabolieten op de fotosynthese (Kropff, 1989) is gebruikt om gegevens over het effect van SO_2 op de fotosynthese tijdens en na een begassingsperiode te analyseren met standaard statistische technieken. De waarde voor de parameter die de relatie tussen S(IV) en fotosynthese karakteriseert en de waarde van de tijdconstante voor de S(IV)-oxidatie werden voor verschillende data-sets over het verloop van de fotosynthese tijdens en na begassing met SO_2 geschat.

De snelle reductie van de fotosynthese na de start van de begassing, het stabiliseren na 1 uur en het snelle herstel na de begassing werden zeer goed met het model beschreven voor de data-sets. De waarden voor de parameters bleken vergelijkbaar met gegevens uit biochemische analyses. Verschillen in gevoeligheid tussen planten voor SO_2 blijken met name te berusten op verschillen in de snelheid waarmee S(IV) wordt geoxideerd. Variatie in bladdikte kan daarnaast van belang zijn geweest. De benadering kan worden gebruikt om inzicht te krijgen in biochemische karakteristieken die de effecten van SO_2 bepalen, met behulp van relatief eenvoudig te verkrijgen data-sets.

References

Alscher, R., Bower, J.L. & Zipfel, W., 1987. The basis for different sensitivities of photosynthesis to SO_2 in two cultivars of pea. Journal of Experimental Botany 38: 99-108.

Alvey, N., Galwey, N. & Lane, P., 1982. An introduction to Genstat. Academic Press, London, New York, 152 pp.

Bennett, J.H. & Hill, A.C., 1973. Inhibition of apparent photosynthesis by air pollutants. Journal of Environmental Quality 2: 526-530.

Black, V.J. & Unsworth, M.H., 1979. Resistance analysis of sulphur dioxide fluxes to *Vicia faba*. Nature 282: 68-69.

Carlson, R.W., 1983. The effect of SO_2 on photosynthesis and leaf resistance at varying concentrations of CO_2. Environmental Pollution (series A) 30: 309-321.

Darrall, N.M., 1986. The sensitivity of net photosynthesis in several plant species to short-term fumigation with sulphur dioxide. Journal of Experimental Botany 37: 1313-1322.

Huber, K., Esterbauer, H., Jäger, H.-J. & Grill, D., 1987. Detection of sulphite in plants. Environmental Pollution (series A) 46: 127-136.

Kropff, M.J., 1987. Physiological effects of sulphur dioxide. 1. The effect of SO_2 on photosynthesis and stomatal regulation of *Vicia faba* L. Plant, Cell and Environment 10: 753-760.

Kropff, M.J., 1989. Modelling short-term effects of sulphur dioxide. 1. A model for the flux of SO_2 into leaves and effects on leaf photosynthesis. Netherlands Journal of Plant Pathology 95 (1989): 195-213.

Miller, J.E. & Xerikos, P.B., 1979. Residence time of sulphite in SO_2 'sensitive' and 'tolerant' soybean cultivars. Environmental Pollution (series A) 18: 259-264.

Rothermel, B. & Alscher, R., 1985. A light-enhanced metabolism of sulphite in cells of *Cucumis sativus* L. cotyledons. Planta 166: 105-110.

Sakaki, T. & Kondo, N., 1985. Inhibition of photosynthesis by sulphite in mesophyll protoplasts isolated from *Vicia faba* L. in relation to intracellular sulphite accumulation. Plant and Cell Physiology 26: 1045-1055.

Sij, J.W. & Swanson, C.A., 1974. Short-term kinetic studies on the inhibition of photosynthesis by sulphur dioxide. Journal of Environmental Quality 3: 103-107.